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1 **Title:** A critical analysis of regulated river ecosystem responses to managed environmental flows  
2 from reservoirs.

3  
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10  
11 **Keywords:** ecosystem response, environmental flows, reservoir

12  
13 **Summary**

- 14  
15 1. The flow regime of a river is fundamental in determining its ecological characteristics.  
16 Impoundment of rivers has been documented to severely impact the natural flow regime, resulting  
17 in abiotic and biotic changes in downstream ecosystems. Contemporary water legislation is driving  
18 increasing concern among environmentalists and water resource managers with respect to how these  
19 impacts can be mitigated. This has stimulated research aimed at assessing the relationship between  
20 reservoir outflow modification (i.e. managed environmental flows) and downstream ecosystem  
21 responses.
- 22 2. We carried out a critical review and synthesis of the global literature concerning post-  
23 impoundment reservoir outflow modification and associated downstream biotic and abiotic  
24 responses. Seventy- six studies published between 1981 and 2012 were analysed. In contrast to  
25 previous studies of this subject, we systematically assessed the methodological quality of research  
26 to identify strengths and weaknesses of the approaches. We also undertook a novel quantification of  
27 ecosystem responses to flow modification, thus enabling identification of priorities for future  
28 research.
- 29 3. We identified that: (i) there was a research bias towards North American and Western European  
30 studies; (ii) the majority of studies reported changes in flow magnitude (e.g. artificial floods) and  
31 primarily focused on traditionally monitored ecological groups (e.g. fish); (iii) relationships  
32 between flow, biota (e.g. macroinvertebrates) and water quality (e.g. electrical conductivity and  
33 suspended solids concentration) were evident, demonstrating the potential for managed  
34 environmental flows to manipulate river ecosystems; (iv) site-specific factors (e.g. location,  
35 climate) are likely to be important as some ecosystem responses were inconsistent between studies

36 (e.g. fish movement in response to increases in flow magnitude); and (v) quality of study design,  
37 methodological and analytical techniques varied, and these factors may have contributed to the  
38 reported variability of ecosystem response.

39 4. To advance scientific understanding and guide future management of regulated flow regimes, we  
40 highlight a pressing need for: (i) diversification of study locations as well as flow modification and  
41 ecosystem response types assessed; (ii) a focus on understanding flow–ecosystem response  
42 relationships at regional scales; (iii) further quantitative studies to enable robust statistical analyses  
43 in future meta-analyses; and (iv) robust monitoring of flow experiments and the use of  
44 contemporary statistical techniques to extract maximum knowledge from ecological response data.

45

## 46 **Introduction**

47

48 The flow regime of a river is fundamental in determining its ecological characteristics (Power et al.,  
49 1995; Poff et al., 1997; Bunn & Arthington, 2002; Olden & Poff, 2003; Allan & Castillo, 1995;  
50 Naiman et al., 2008). Flow influences the abundance and distribution of lotic species (Allan &  
51 Castillo, 1995) both indirectly through physical habitat modification and directly through  
52 stimulation of biotic responses (Bunn & Arthington, 2002; Milner et al., 2013) [e.g. movement  
53 (James, Dewson & Death, 2008) and spawning (Gorski et al., 2010)]. The natural flow regime  
54 paradigm stresses that the natural characteristics of a flow regime are critical in maintaining  
55 ecological integrity (Poff et al., 1997), as the two are intrinsically linked having evolved together  
56 over time (Lytle & Poff, 2004). Ecological integrity is increasingly the focus of contemporary  
57 freshwater legislation (e.g. Clean Water Act, 2002; EU Water Framework Directive (EU WFD)  
58 (EC, 2000); Water Act, 2007), stimulating a desire to identify and understand river flow–ecosystem  
59 response relationships. This understanding is crucial for effective management of freshwater  
60 ecosystems (Tharme, 2003; Olden & Naiman, 2010; Shafroth et al., 2010; Rolls & Arthington,  
61 2014) which is recognised as one of civilisation’s greatest contemporary challenges (Palmer et al.,  
62 2004; Vorosmarty et al., 2010; Naiman & Dudgeon, 2011).

63

64 River impoundment has been documented to severely impact characteristics of the natural flow  
65 regime, primarily through the reduction and redistribution of flow throughout time (Petts, 1984;  
66 Higgs & Petts, 1988; Nilsson et al., 2005). Globally, these impacts have been well documented; for  
67 example, Petts (1984) stated that mean annual discharge can be reduced by up to 80%, seasonal  
68 flow variability can be reduced, and the timing of annual extremes in flow can be altered. Annual  
69 peak discharges can be reduced by up to 90%, in some cases (Graf, 2006). General modifications of  
70 natural flow regime characteristics (including physicochemical modifications) have been associated

71 with impacts to downstream ecosystems. Poff & Zimmerman (2010) found that 92% of studies  
72 reported reductions in ecological metrics in response to all anthropogenic flow modifications.  
73 Specifically, impacts to morphology (e.g. Petts & Pratts, 1983; Petts, Armitage & Castella, 1993;  
74 Sear, 1995; Shields, Simon & Steffen, 2000; Petts & Gurnell, 2005; Wellmeyer, Slattery & Phillips,  
75 2005 and Xu et al., 2006), water quality (temperature: Baxter, 1977; Petts, 1984; Todd et al., 2005;  
76 Olden & Naiman, 2010; dissolved metal concentrations: Petts, 1984 and oxygen: e.g. Lutz, 1995)  
77 and biota, including primary producers (e.g. Jones & Barrington, 1985), macrophytes (e.g. Garcia  
78 De Jalon, Sanchez & Camargo, 1994 and Bernez et al., 2004), macroinvertebrates (e.g. Englund &  
79 Malmqvist, 1996; Grown & Grown, 2001 and Gillespie, Brown & Kay, 2014) and fish (e.g. Baran  
80 et al., 1995; Linnik et al., 1998 and Korman, Wiele & Torizzo, 2004) have been observed as a result  
81 of river impoundment. A drive to mitigate these impacts through reservoir outflow modification has  
82 recently been stimulated. These interventions are commonly described as ‘environmental flows’,  
83 and it is clear that their implementation will be vital to meet the aims of contemporary legislation  
84 [e.g. the Australian National Water Initiative (Connell & Grafton, 2008) and the EU WFD  
85 (Acreman & Ferguson, 2010)].

86

87 Environmental flows have been defined as ‘the quantity, timing, duration, frequency and quality of  
88 water flows required to sustain fresh water, estuarine and near-shore ecosystems and the human  
89 livelihoods and well-being that depend on them’ (Acreman & Ferguson, 2010, p. 32). More  
90 specifically, Acreman et al. (2009, p. 15) suggested that environmental flows should ‘be based on  
91 ecological requirements of different communities/ species/life stages, which may vary within and  
92 between rivers even for the same biological elements or communities’. It is clear that to define  
93 environmental flows for regulated rivers, identification of cause–response relationships between  
94 flow modification and ecosystem response variables must be achieved (Shafroth et al., 2010). Such  
95 relationships have been hypothesised (Poff et al., 2010), but a synthesis of the global literature  
96 offers the potential to identify and quantify them.

97

98 Poff & Zimmerman (2010) have analysed the global literature on the ecological effects of altered  
99 flow regimes (often as a consequence of water storage in dams and water release patterns  
100 downstream). However, to date, no study has attempted to identify general relationships between  
101 flow modification interventions (e.g. artificial floods and other types of environmental flows) and  
102 ecological responses from the global literature.

103

104 A systematic synthesis of the global literature would allow for an evaluation of abiotic and biotic  
105 responses to managed environmental flows and facilitate identification of prominent knowledge

106 gaps and prioritisation of future research agendas. Such insights and guidance would be useful  
107 given the relatively early stage of development and growing importance of the science of  
108 environmental flows (Tharme, 2003; Reich et al., 2010; Davies et al., 2014). It was envisaged that  
109 our study would build on recent reviews concerning the impacts of managed environmental flows  
110 (i.e. Konrad et al., 2011; Olden et al., 2014). Konrad et al. (2011) drew on case studies to identify  
111 challenges surrounding flow experimentation and proposed key principles to attain success in future  
112 flow experiments. Olden et al. (2014) then objectively catalogued and evaluated in broad terms the  
113 success of flow experiments globally. We propose that the next logical step should be an attempt to  
114 generalise flow modification– ecological response relationships from the literature and evaluate the  
115 quality of data underpinning these relationships. Thus, our study aims were to identify downstream  
116 ecosystem responses to managed environmental flows, quantify flow–response relationships and  
117 evaluate current research methods and study designs to prioritise and enhance future research  
118 agendas.

119

## 120 **Methods**

121

### 122 *Literature search*

123

124 Relevant published literature was located through computerised searches of ISI Web of Knowledge  
125 which includes the following databases: Web of Science (1990– present), BIOSYS Citation Index  
126 (1969–present), BIOSYS Previews (1969–present), Data Citation Index (1900– present),  
127 MEDLINE (1950–present) and Journal Citation Reports. Table 1 lists the search terms used and  
128 number of results returned. All searches were undertaken in July 2012 by a single reviewer, and a  
129 total of 3,981 records were assessed for suitability through attainment of the following criteria: (i)  
130 reported primary data; (ii) assessed the impact of modification of the outflow regime of a reservoir;  
131 (iii) focused on impacts to instream ecosystems (biotic and abiotic elements) downstream of the  
132 reservoir; and (iv) were published in academic journals and had thus undergone peer review (cf.  
133 Olden et al. (2014) who also incorporated grey literature). The latter criterion was considered to be  
134 particularly important given our emphasis on data extraction and meta-analysis, because  
135 incorporation of data sets contained only in grey literature may inhibit any future reassessments due  
136 to restricted access for other authors.

137

### 138 *Data extraction and quality assessment*

139

140 First, the study location(s) (reservoir where flow modification was made) reported in each study

141 were recorded and mapped to assess any spatial patterns or biases in the literature. Next, ecosystem  
142 responses to flow modification highlighted in each study were recorded and categorised as either  
143 biotic or abiotic. To specifically build on the work of Olden et al. (2014), biotic changes were  
144 assigned to either reduced, no change or increased response categories to allow for comparison of  
145 general trends (see Poff & Zimmerman, 2010). For example, increased macroinvertebrate diversity  
146 in response to flow modification was classified as an increased response. Likewise, a reduction in  
147 fish movement in response to flow modification was classified as reduced response. Additionally,  
148 biotic responses were split into native or non-native/ invasive groups where detail was given as each  
149 group may respond differently to flow modification (e.g. Cross et al., 2011). Abiotic responses were  
150 assigned to either change or no change categories as reductions or increases in abiotic parameters  
151 may be less comparable than for biotic responses (e.g. increased temperature and electrical  
152 conductivity (EC) are less likely to both be either ecologically 'good' or 'bad' than increased fish  
153 and macroinvertebrate abundance). To enable further breakdown of the types of responses  
154 researched, ecosystem responses were assigned to either: (i) fish; (ii) macroinvertebrates; (iii)  
155 macrophytes; (iv) primary producers (benthic); (v) morphology; (vi) water quality (including  
156 suspended sediment transport); and (vii) other categories.

157  
158 Flow modification can often be classified as more than one type of response; for example, a flow  
159 modification from a reservoir may result in both an increase in magnitude and duration (Poff et al.,  
160 1997). Thus, to classify the type of flow modification each ecosystem response was associated with,  
161 we recorded the element of flow modification that was most emphasised by each study (following  
162 Poff & Zimmerman, 2010) using the characteristics listed as ecologically important by Poff et al.  
163 (1997). This approach differs to that of Olden et al. (2014) where flows were categorised based on  
164 management aim (e.g. operating regime; change in release mode). Ecosystem responses have been  
165 observed to vary depending on whether they arise as a result of a single, or a series of flow  
166 modifications (e.g. Uehlinger et al., 2003). Thus, to allow for separate analysis of these two  
167 modification types, ecosystem responses were further classified by whether they were reported as a  
168 result of a single or series of cumulative flow modifications. Ecosystem responses within each  
169 category were then synthesised, and commonly reported responses were tabulated. To allow for  
170 clear tabulation of results, a frequency of observation of at least four was selected to represent a  
171 'common' observation.

172  
173 In an attempt to produce quantitative relationships between reservoir outflow modification and  
174 ecosystem responses, first, we identified studies where a single flow modification and associated  
175 ecosystem response could be represented as percentage change. Of the 76 studies identified in the

176 literature search, this was possible for 20; although some studies reported on more than one flow  
177 modification or ecosystem response, resulting in 119 observations of flow modification to  
178 ecosystem response being extracted in total. From initial analysis of data points, all observed  
179 ecosystem responses were a result of modification of flow magnitude. We thus defined percentage  
180 change for each flow modification using Equation 1, where  $x_1$  was pre-flow modification discharge  
181 magnitude and  $x_2$  was maximum (or minimum in the case of a reduction in magnitude) discharge  
182 magnitude of the flow modification. Equation 1 was also used for calculation of percentage change  
183 in ecosystem response, where  $x_1$  was pre-flow modification condition and  $x_2$  was either condition  
184 of maximum change from  $x_1$  (if sampling was undertaken during flow modification) or condition  
185 immediately after the flow modification (if sampling was undertaken after the flow modification). If  
186 possible, data were extracted from the text/tables and alternatively from figures. For response  
187 variables, where sampling was replicated, we used mean values and where non-significant  
188 responses were noted, we recorded percentage change as zero.

189

$$190 \quad \text{Percent change} = \left( \frac{x_2 - x_1}{x_1} \right) \times 100 \quad \text{(Equation 1)}$$

191

192 To visualise flow–ecosystem response relationships, data points were organised by response type  
193 using the seven categories employed in qualitative data extraction and, where more than five data  
194 points reported on the same ecosystem response, plots of flow (percentage change) versus  
195 ecosystem response (percentage change) were created. For some ecosystem response types,  
196 visualisation revealed broadly linear relationships; the significance of these relationships was  
197 assessed using generalised linear models (GLM) with appropriate error distribution and link  
198 functions specified. Statistical analysis of fewer than 10 data points has been regarded as invalid  
199 (Roscoe, 1975); therefore, we carried out modelling only where a minimum of 10 data points had  
200 been extracted. Model validation was carried out to ensure approximate normal distribution and  
201 homogeneity of residuals. Significance of relationships was assessed through consideration of t-  
202 statistics and associated P values (e.g. Zuur et al., 2009). All visualisations and statistical analyses  
203 were undertaken in R v2.15.3 (2013), and relationships were considered significant at  $P < 0.05$ .

204

205 In their proposed principles for successful flow experiments, Konrad et al. (2011) cited study design  
206 and methodological approaches (e.g. control sites; replication) as important. To allow assessment of  
207 current research standards and to support recommendations to enhance future research strategies,  
208 we recorded: (i) the type(s) of sampling strategy used to detect ecosystem responses (quantitative,  
209 semi-quantitative or qualitative); (ii) whether randomisation or replication was applied in sampling

210 designs; (iii) type(s) of control sites used (if any) (e.g. upstream of reservoir; nearby unregulated  
211 river); (iv) analytical approaches applied in each study; and (v) whether statistical power was  
212 reported.

213

## 214 **Results**

215

216 Most studies were located within North America and western Europe and a dearth of study locations  
217 was observed within equatorial regions, South America, north Africa, Asia and eastern Europe (Fig.  
218 1A). Two study locations had notably high densities of work: Lake Powell (Glen Canyon Dam),  
219 U.S.A. and Lago di Livigno (Punt dal Gall Dam), Switzerland/ Italy (Fig. 1B).

220

### 221 *Qualitative analysis of assembled datasets*

222

223 The majority of studies (n = 69) focused on modified flow magnitude, with very few studies  
224 reporting on changed reservoir draw-off valve (n = 1), modified flow duration (n = 2), range (n = 2)  
225 and rate of change (n = 2) (Fig. 2). Studies reporting fish response were the most frequent (n = 28)  
226 and a relatively high number of studies reported on water quality and macroinvertebrate responses  
227 (n = 27 and 19, respectively). In contrast, few studies reported on macrophytes and primary  
228 producers (n = 3 and 12, respectively) (Fig. 3). Fifty-five and 21 studies reported ecosystem  
229 responses as a result of single or cumulative modifications in flow magnitude, respectively.  
230 However, only seven studies reported ecosystem responses associated with either rate of flow  
231 change, duration, range and draw-off depth from the reservoir (Table 2).

232

233 Numerous studies detailing ecosystem responses as a result of flow magnitude modification  
234 reported increased biotic responses (n = 35), although a similar number of studies reported  
235 decreased or no change in biotic response (n = 30 and 25, respectively). This trend was mirrored in  
236 ecosystem responses as a result of single flow magnitude modification; however, as a result of  
237 cumulative modifications in flow magnitude, the majority of studies reported decreased biotic  
238 responses (Table 2). Single modifications of flow magnitude were commonly reported to result in:  
239 (i) both increased and no change in fish movement (during flow modification); (ii) no change in fish  
240 abundance (after flow modification); and (iii) increased macroinvertebrate drift (during flow  
241 modification) and reduced macroinvertebrate density (after flow modification). Similarly,  
242 cumulative modifications of flow magnitude were associated with reduced macroinvertebrate  
243 density and, additionally, reduced periphyton mass (after flow modification).

244



245 The majority of studies reported changes in abiotic condition as a result of both single and  
246 cumulative modifications in flow magnitude. Common responses were identified as: (i) increased  
247 turbidity, suspended solids concentration (SSC) and bedload transport (during flow modification);  
248 (ii) reduced EC (during flow modification); and (iii) both no change and an increase in river  
249 temperature (during flow modification) (Table 2). Due to the limited number of studies reporting  
250 ecosystem changes as a result of other flow modification types (i.e. rate of flow change, duration,  
251 range and draw-off depth), generalisations of ecosystem response associated with these flow  
252 modification types could not be made.

253

#### 254 *Quantitative analysis of assembled datasets*

255

256 Periphyton AFDM, chlorophyll-a, benthic macroinvertebrate density, seston AFDM and  
257 chlorophyll- a either decreased or showed no change after increased flow magnitude (Fig. 4a,c).  
258 Macroinvertebrate drift and concentrations of Escherichia coli either increased or did not change  
259 during increased flow magnitude (Fig. 4b,d). No clear trends in response direction or flow  
260 thresholds could be identified for any biotic response.

261

262 River EC was generally reduced during increased flow magnitude, and a general negative linear  
263 relationship was observed (Fig. 4e). Conversely, SSC generally increased during increased flow  
264 magnitude; however, this relationship was not significant ( $t = -1.50$ ,  $P = 0.16$ ). No clear trend was  
265 observed for turbidity (Fig. 4f).

266

#### 267 *Quality assessment*

268

269 Seventy-one, 14 and three studies used fully, semi-quantitative or qualitative methods, respectively,  
270 to assess ecosystem response to flow modification. Forty-seven studies described replication in  
271 sampling, whilst only 19 stated randomisation. Fully quantitative methods of fish and macrophyte  
272 assessment were used in fewer than 60% of cases, whereas over 85% of assessments were fully  
273 quantitative for all other ecosystem response types. Qualitative methods were only used for  
274 assessment of fish and macrophytes (6 and 33%, respectively). Whereas over 90% of assessments  
275 of water quality response were fully quantitative, fewer than 5% were stated as either replicated or  
276 randomised. Randomised sampling was stated in 50% of primary production assessments, whilst  
277 fewer than 25% of sampling designs for all other ecosystem responses were described as  
278 randomised. Over 50% of assessments of fish, macroinvertebrate and primary production response  
279 were defined as replicated, compared to fewer than 5% of assessments of water quality (Fig. 5).

280

281 Only 14 studies stated use of control sites, and of these, 10 used nearby unregulated rivers, five used  
282 controls upstream of the reservoir and one used a regulated (with unmodified flow) control (note:  
283 some studies used more than one control type). Thirty-four studies used descriptive or graphical  
284 methods to present results (i.e. no statistical testing), and 10 studies used correlation or regression  
285 between a metric of flow and ecosystem response. Twenty-eight studies assessed the impact of flow  
286 modification through comparison of ecosystem conditions either through time or between  
287 impact/control sites using simple one-way or two-way testing (e.g. Student's t-test; Mann–Whitney  
288 U-test; ANOVA; Kruskal–Wallis test). Six studies used alternative methods: multiple linear/least  
289 linear squares/polynomial regression, general linear/additive/generalised linear mixed modelling.  
290 Only three studies tested site:period interaction terms as part of Before–After Control–Impact  
291 (BACI) (or derivations of) (Smith, 2002) designs, and only eight studies used analytical methods  
292 that took account of temporal autocorrelation. It was also identified that just two studies (Meissner,  
293 Muotka & Kananen, 2002; Rolls et al., 2011) noted statistical power of their methods.

294

## 295 **Discussion**

296

### 297 *Spatial distribution of studies*

298

299 The spatial distribution of studies found by this study was generally in agreement with Olden et al.  
300 (2014), further emphasising the requirement for research in areas where reservoir density is high  
301 and published research is currently limited (i.e. Eastern Europe, Asia, central eastern South America  
302 and Central and South Africa). This observed research bias should be taken into account when  
303 considering the global applicability and relevance of our findings.

304

### 305 *Flow and ecosystem response types*

306

307 Our finding that the majority of studies reported flow modification as an expression of change in  
308 magnitude was accordant with those of Poff & Zimmerman (2010) and Olden et al. (2014). We  
309 propose that this may be due to increased flow magnitude being the most perceptible element of  
310 change during flow modification, where changes in alternative flow elements (e.g. rate of change,  
311 timing) are more subtle, but still occur. Future publications reporting impacts of flow modification  
312 should take care to highlight all elements of hydrological change associated with measured  
313 ecosystem responses to enable scrutiny and integration of all flow–ecosystem relationships in  
314 subsequent reviews. Low flows are critical in determining ecosystem integrity in natural rivers (Poff

315 et al., 1997; Ledger et al., 2013), but further analysis of our data set revealed that only one study  
316 reported on a reduction in flow magnitude (Saltveit et al., 2001; who found that fish stranding  
317 occurred as a result of rapid reductions in flow), whilst all other studies concerning changes in  
318 magnitude reported on increased flow magnitude. The impact of reduction in flow magnitude in  
319 regulated rivers is a key priority for future research as, for example, typical compensation flows in  
320 the U.K. were set, on average, over 22% higher than pre-impoundment natural low flows (Gustard,  
321 1989). Given the importance of all trophic levels in sustaining freshwater ecological integrity  
322 (Parrish, Braun & Unnasch, 2003), the bias towards monitoring of traditional indicator taxa (e.g.  
323 fish) is a concern. This finding was also found by Olden et al. (2014), and there is therefore a clear  
324 need for diversification of monitoring strategies to cover less typically monitored taxa in future  
325 studies.

326

### 327 *Qualitative and quantitative flow-ecosystem response relationships*

328

329 A novel objective of this review, cf. preceding papers on the subject of flow experiments, was to  
330 extract, synthesise and evaluate ecosystem responses to reservoir outflow modification primarily  
331 designed to reduce/alleviate the impacts of flow regime alterations downstream from reservoirs. It  
332 was expected that this would reveal general flow–ecosystem response relationships for regulated  
333 rivers and highlight future research priorities, ultimately aiding advancement of the science of  
334 regulated river management.

335

#### 336 *Qualitative*

337

338 The majority of flow magnitude modifications resulted in either increased or decreased ecosystem  
339 responses, demonstrating that reservoir flow magnitude modification is a potentially useful option  
340 to modify some ecological features in regulated rivers. However, no clear trend in biotic response to  
341 all, single and cumulative flow magnitude modifications was identified, suggesting the importance  
342 of site-specific factors. For example, it was found that in response to single increased flow  
343 magnitude events, seven studies reported no change in, and six studies reported increased fish  
344 movement (Table 2). These contradictory observations may be explained by a combination of  
345 factors, for example: the characteristics of the flow modification (e.g. percentage increase, rate of  
346 change); the characteristics of the fish monitored (e.g. species, size, flow preference); and additional  
347 abiotic factors such as season, antecedent flow conditions, instream habitat type, time since  
348 impoundment, time elapsed between flow modification and measurement of ecological responses.  
349 To enable a more robust analysis of these relationships, details on these potentially confounding

350 factors must be considered in each study. We were unable to extract these data for this review, and  
351 future publications should therefore consider including detailed information on all potentially  
352 relevant factors.

353

354 Our qualitative analysis revealed some general trends in macroinvertebrate response: increased drift  
355 (during flow modification) and reduced benthic densities were results of both single and cumulative  
356 increases in flow magnitude (Table 2). Benthic macroinvertebrate density commonly increases post-  
357 impoundment (Petts, 1984), suggesting that increased flow magnitude events have potential to  
358 mitigate for this impact. Importantly though, some studies have noted a quick recovery from single  
359 flow magnitude modifications (e.g. Jakob, Robinson & Uehlinger, 2003) which suggests that one-  
360 off flow modification events may not be viable long-term mitigation methods. However,  
361 understanding of long-term responses of macroinvertebrates to reservoir flow modification is  
362 spatially limited (e.g. Robinson, Uehlinger & Monaghan, 2004; Mannes et al., 2008; Robinson &  
363 Uehlinger, 2008) and is a topic that requires further research globally.

364

365 We identified that the vast majority of flow magnitude modifications resulted in abiotic changes,  
366 specifically, increased turbidity, SSC and bedload transport (Table 2). This suggests that flow  
367 magnitude modification has potential for use in mitigation of the effects of impoundment such as  
368 reduced sediment transport (Petts, 1984; Petts & Gurnell, 2005). No studies were found that  
369 highlighted the long-term impact of flow magnitude modification on sediment transport as all  
370 sampling was undertaken during each event. We therefore recommend future research aims to  
371 assess how river sediment transport responds both during and after single and cumulative flow  
372 magnitude modifications.

373

374 Our qualitative analysis of physicochemical factors revealed that increased flow magnitude  
375 commonly resulted in reduced EC. Heterogeneity in concentrations of dissolved ions is typical in  
376 natural lotic systems (e.g. Glover & Johnson, 1974), thus increased flow magnitude events have the  
377 potential to mitigate reduced EC temporal variability observed post-impoundment (e.g. Palmer &  
378 O’Keeffe, 1990). It was also found that water temperature was commonly observed to decrease or  
379 not change as a result of increased flow magnitude; this is most likely due to site-specific climatic  
380 and reservoir characteristics and the vertical position of the draw-off valve used during flow  
381 modification. One study (Macdonald, Morrison & Patterson, 2012) found that draw-off level from  
382 the reservoir was a significant factor in determining downstream temperature. The potential for  
383 temperature modification through reservoir flow operation (see Olden & Naiman (2010) for  
384 discussion) is evident, which may be important given the crucial influence of temperature on biota

385 in freshwater systems (Cummins, 1974; Beschta et al., 1987; Webb et al., 2008) and the significant  
386 impact of reservoirs on downstream thermal regimes (Petts, 1984; Dickson, Carrivick & Brown,  
387 2012). Further research should be directed towards assessment of the relative importance of  
388 different flow modification types in controlling downstream temperature, especially the impact of  
389 reservoir draw-off level which, to date, has received little attention.

390

#### 391 *Quantitative*

392

393 No clear trends were observed between flow magnitude modification and biotic responses, most  
394 likely reflecting minimal availability of data points and the importance of site-specific factors. For  
395 example, Robinson (2012) identified clear relationships between flood magnitude and biotic  
396 response for flow modification events for one river, but in our meta-analysis incorporating data  
397 from multiple locations, this relationship was not evident. Approximately linear relationships were  
398 found between percentage changes in flow magnitude modification and EC (negative relationship)  
399 and SSC (positive relationship), demonstrating the potential for manipulation of the magnitude of  
400 reservoir flow releases as a river management technique. The lack of statistical significance for the  
401 flow modification and SSC relationship indicates the potential importance of site-specific factors  
402 (e.g. local geology, characteristics of flow modification, antecedent flow). In accordance with Poff  
403 & Zimmerman (2010), no threshold flow changes (where abrupt changes in ecological response  
404 could be identified) were observed for these parameters, potentially due to the lack of thresholds,  
405 and/or the lack of quantitative data points with which to identify them (Poff & Zimmerman, 2010;  
406 Poff et al., 2010). Uncertainty around this issue warrants further research attention given the  
407 potential importance of such information for river managers (Richter et al., 2003).

408

409 Our review was carried out using a similar method to Poff & Zimmerman's (2010) review of  
410 ecological response to flow regulation. The authors concluded that their focus on all river types and  
411 all types of modification (e.g. dam construction, irrigation and urbanisation leading to increased  
412 run-off) may have limited their ability to find general flow–ecosystem response relationships. Our  
413 review differed in that it focussed specifically on reservoir outflow modification post-impoundment  
414 (Table 3) in an attempt to address this limitation. However, similar to Poff & Zimmerman (2010),  
415 we found that our analysis was restricted by both the small number of data points and the limited  
416 information we were able to extract relating to potential confounding factors (Table 3). As  
417 development of flow–ecosystem response relationships in reservoir regulated rivers increases over  
418 time, we suggest that future research would benefit by analysing these relationships collectively  
419 between areas of similar climatological and geological characteristics, as these factors are expected

420 to influence ecosystem response to flow modification (Arthington et al., 2006; Poff et al., 2010).  
421 This would further the development of smaller scale, regional or environment 'type' based  
422 relationships which are required for environmental flow setting frameworks such as ELOHA  
423 (Ecological Limits of Hydrological Alteration) (Poff et al., 2010) or the building block  
424 methodology (BBM) (King & Louw, 1998).

425

#### 426 *Quality assessment*

427

428 Over 90% of studies used fully quantitative methods to assess at least one ecosystem response to  
429 flow modification, although method types varied by ecosystem response type. For example, fewer  
430 than 60% of methods were fully quantitative for assessment of fish and macrophytes. A propensity  
431 for semi-quantitative electric fishing techniques (32% of all fish response assessments) and the  
432 limited number of assessments of macrophytes (n = 3) explain this observation. Research has  
433 suggested that semi-quantitative methods of fish sampling to gauge abundance can be up to 95%  
434 accurate (Klein-Breteler, Raat & Grimm, 1990), thus the high proportion of semi-quantitative  
435 methods for assessment of fish response is not a major concern.

436

437 Johnson (2002) describes replication and randomisation as two 'cornerstones' of experimentation  
438 and states that they are integral to successful ecological research; yet, ecologists often commit  
439 replication errors (Hurlbert, 1984) and rarely select study areas or sampling locations randomly  
440 (Johnson, 2002). Our review identified similar trends, as 47 studies (62%) stated that replication  
441 was used in sampling, whilst only 19 (25%) stated randomisation was applied, but interestingly, the  
442 distribution of the use of these techniques was unequal among ecosystem response types. In  
443 particular, fewer than 5% of assessments of water quality responses were stated as either replicated  
444 or randomised, whereas all other ecosystem elements were stated as being assessed using either  
445 replicated or randomised methods in at least 30% of cases. No explanations of why replication or  
446 randomisation had not been carried out for water quality assessment were given. However, the  
447 approaches used may reflect consensus in the literature where replication (Hauer & Hill, 1996;  
448 USEPA, 2004) and randomisation (Hauer & Hill, 1996) are not highlighted as important in water  
449 quality monitoring. We have identified a lack of use of these 'cornerstones' and suggest that future  
450 research integrates both facets.

451

452 The majority of studies used one-way comparisons of sample periods (e.g. before/after flow  
453 modification) or between control/impact sites over sample periods. One of the limitations of these  
454 approaches is that they fail to take account of temporal autocorrelation (only eight studies (11%)

455 took temporal autocorrelation into account) and can result in less robust analysis (Zuur et al., 2009).  
456 BACI designs are recommended methodological frameworks for impact assessment of  
457 anthropologically driven disturbance events (Underwood, 1991) such as flow modifications from  
458 reservoirs. BACI designed experiments allow for significance testing of site:period interaction  
459 terms (see Underwood, 1991) which takes into account variation that is assumed to have occurred if  
460 the impact (e.g. flow modification) had not been undertaken. Nevertheless, only three studies used  
461 this approach and we suggest future researchers consider use of such a technique to assess impacts  
462 of reservoir flow modification. Selection of a control site is necessary when applying BACI  
463 approaches, but only 14 studies (<20%) reported use of control sites. Within these studies,  
464 considerable variability in the 'type' of control site was identified. Currently, research is lacking as  
465 to which 'type' provides the most robust method. However, given that ideal control sites should be  
466 both independent of, but as similar as possible in abiotic and biotic characteristics to, the impacted  
467 site (e.g. McMahon, 2010), it is probable that an independent, regulated control site has the  
468 potential to act as the most effective control. Further research is required to test this hypothesis.

469

470 Reporting of statistical power in scientific research is important as it puts the finding of 'no  
471 significant change' or 'no significant response' in context and allows assessment of the likelihood  
472 of a type II error (Nakagawa, 2004). Just two studies noted the statistical power of their methods,  
473 and we therefore recommend reporting of this statistic in future studies to enable the assessment of  
474 false-negative errors. Such an assessment has the potential to reveal findings which require  
475 clarification and therefore merits further research.

476

477 Our literature search revealed inconsistent use of terms and keywords used to describe research  
478 concerning the impact of reservoir flow modification on downstream ecological conditions. To aid  
479 efficiency of future literature searches, we suggest all future literature concerning this topic includes  
480 the keywords 'environmental flow' and 'reservoir' where possible. The currently accepted  
481 definition of environmental flow is broad and encapsulates topics such as flow distribution in  
482 multicatchment water transfers, canals and wetlands (Dyson, Bergkap & Scanlon, 2003; Arthington,  
483 2014), and thus, the inclusion of 'reservoir' will aid the search process.

484

## 485 **Conclusion**

486

487 This study has synthesised the global literature concerning managed environmental flows and the  
488 associated downstream river ecosystem response. We were able to recognise biases within both the  
489 location of studies and research topics. This study also identified qualitative and quantitative flow–

490 ecosystem response relationships. In particular, as a result of increased flow magnitude,  
491 macroinvertebrate density and drift were commonly identified to decrease and increase,  
492 respectively, and periphyton mass was commonly observed to decrease. Further, during increased  
493 flow magnitude, reduced EC and increased SSC, turbidity and bedload movement were commonly  
494 observed. However, our analyses were constrained by the limited number of quantitative data points  
495 available for analysis of specific flow–ecosystem response relationships. Nevertheless, from our  
496 synthesis, we were able to make a number of recommendations for future work (Table 3). We found  
497 that improvements in research design and analytical methodologies could be made through the  
498 implementation of contemporary techniques. Overall, our findings, together with the  
499 implementation of our recommendations for future research, have the potential to redirect and focus  
500 regulated river science and environmental flow management in a concerted and effective manner.

501

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506

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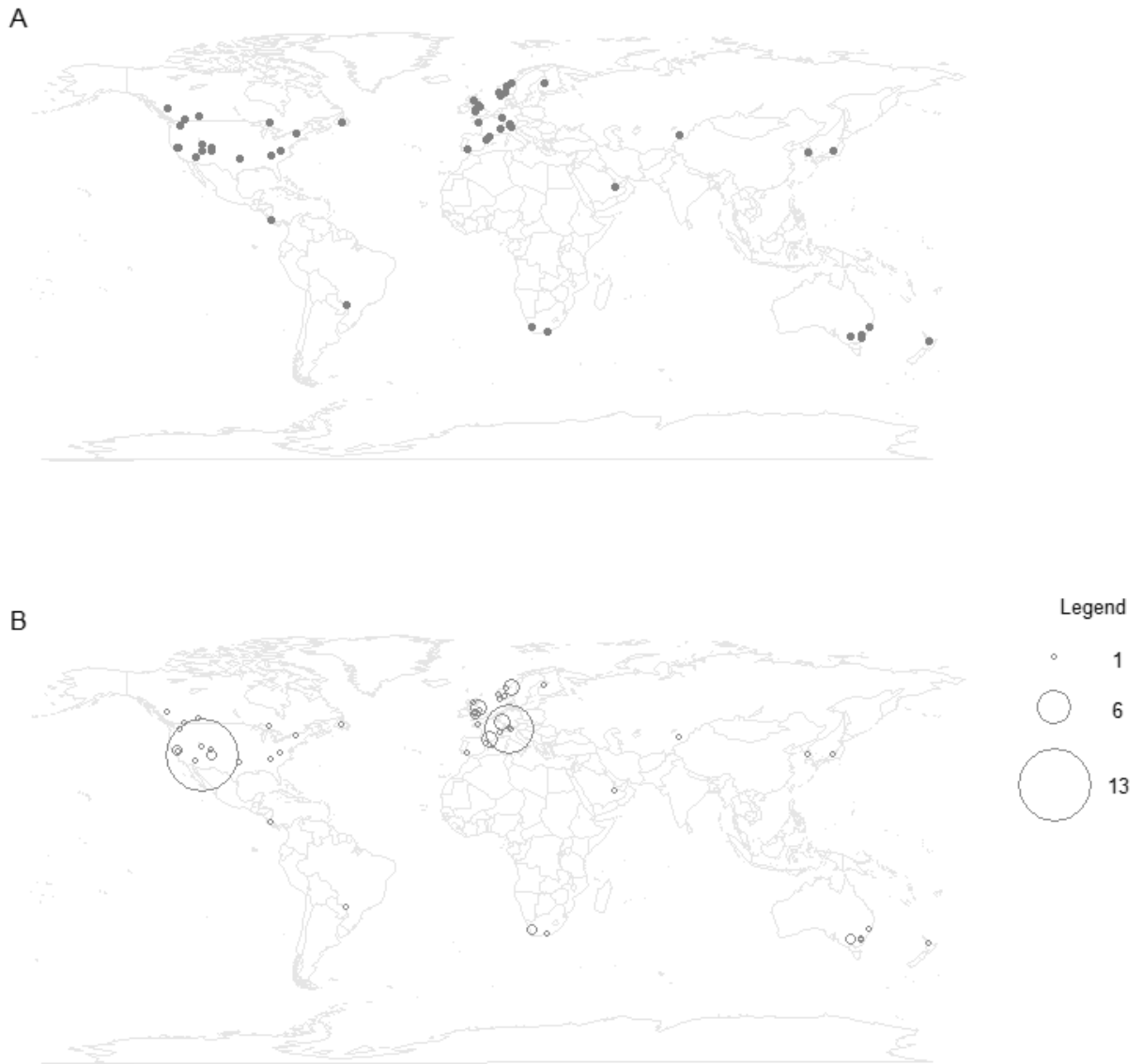
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### 815 **Supporting information**

816

817 *Appendix 1: Studies used in literature review, including study ID, location and ecosystem*  
818 *response type reported by each study and a complete bibliography.*

819



*Figure 1 Location of the 76 studies considered within this review. B: Number of studies considered within this review at each location.*

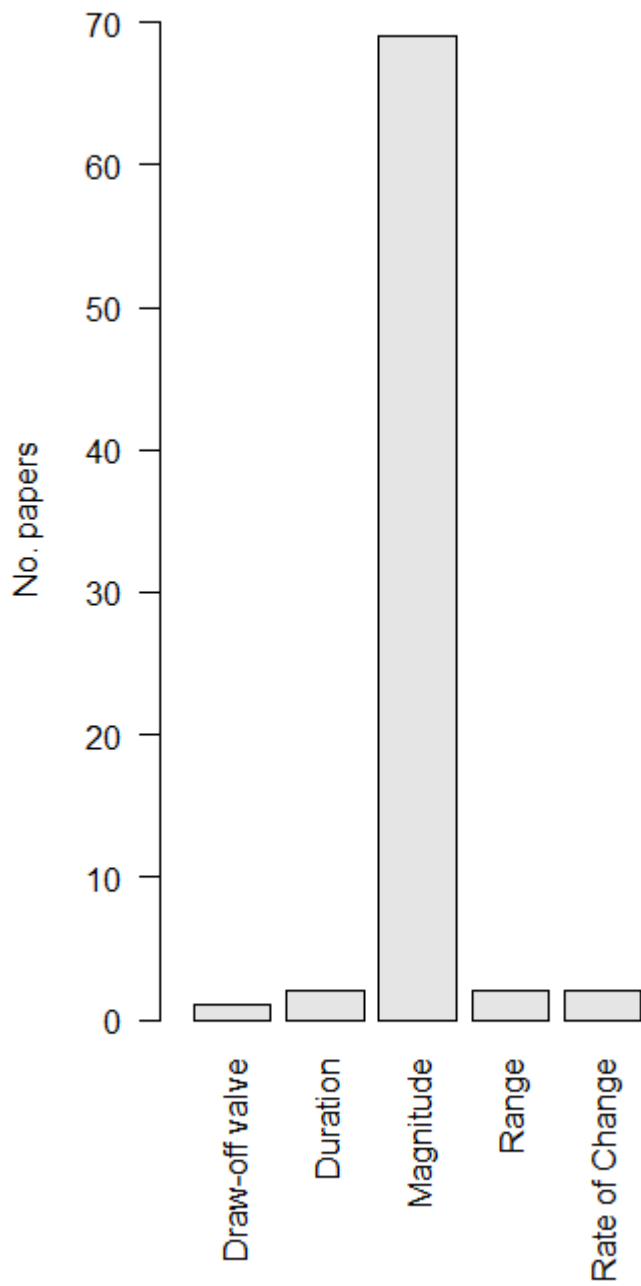
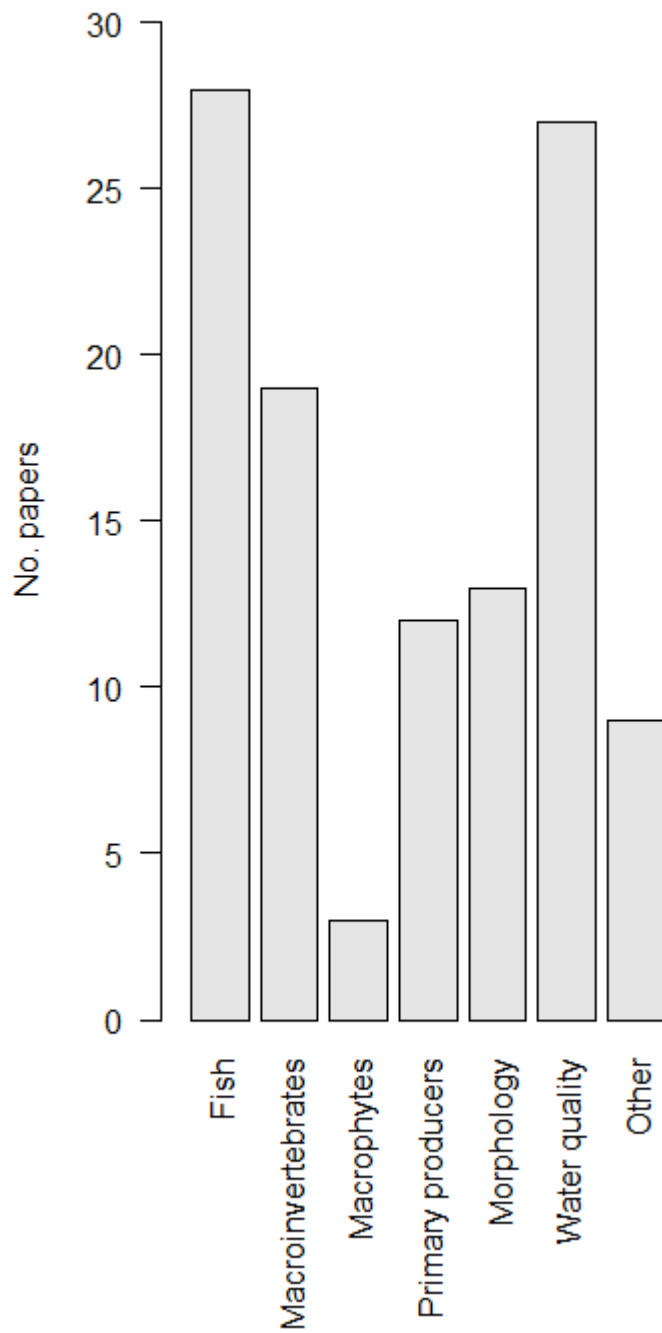


Figure 2 Number of studies (from a total of 76) that reported on each flow modification type.



*Figure 3 Number of studies (from a total of 76) that reported on each ecological response type. N.B. some studies reported on more than one category.*

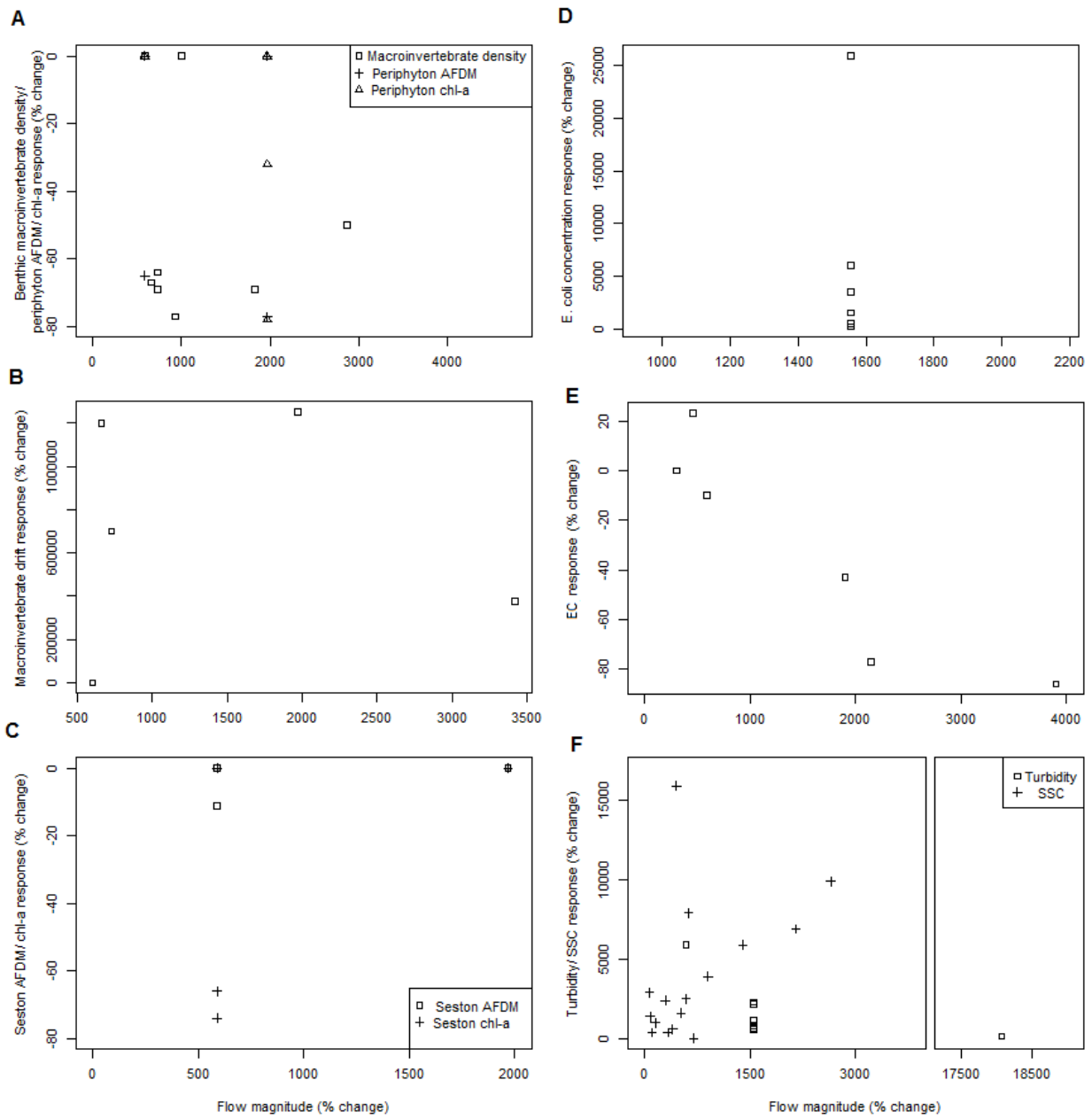


Figure 4 Biotic (A-D) and abiotic (E-F) ecological responses to flow magnitude percent change. N.B. Ecological responses are after- and during-flow modification for plots A-B and C-F, respectively.

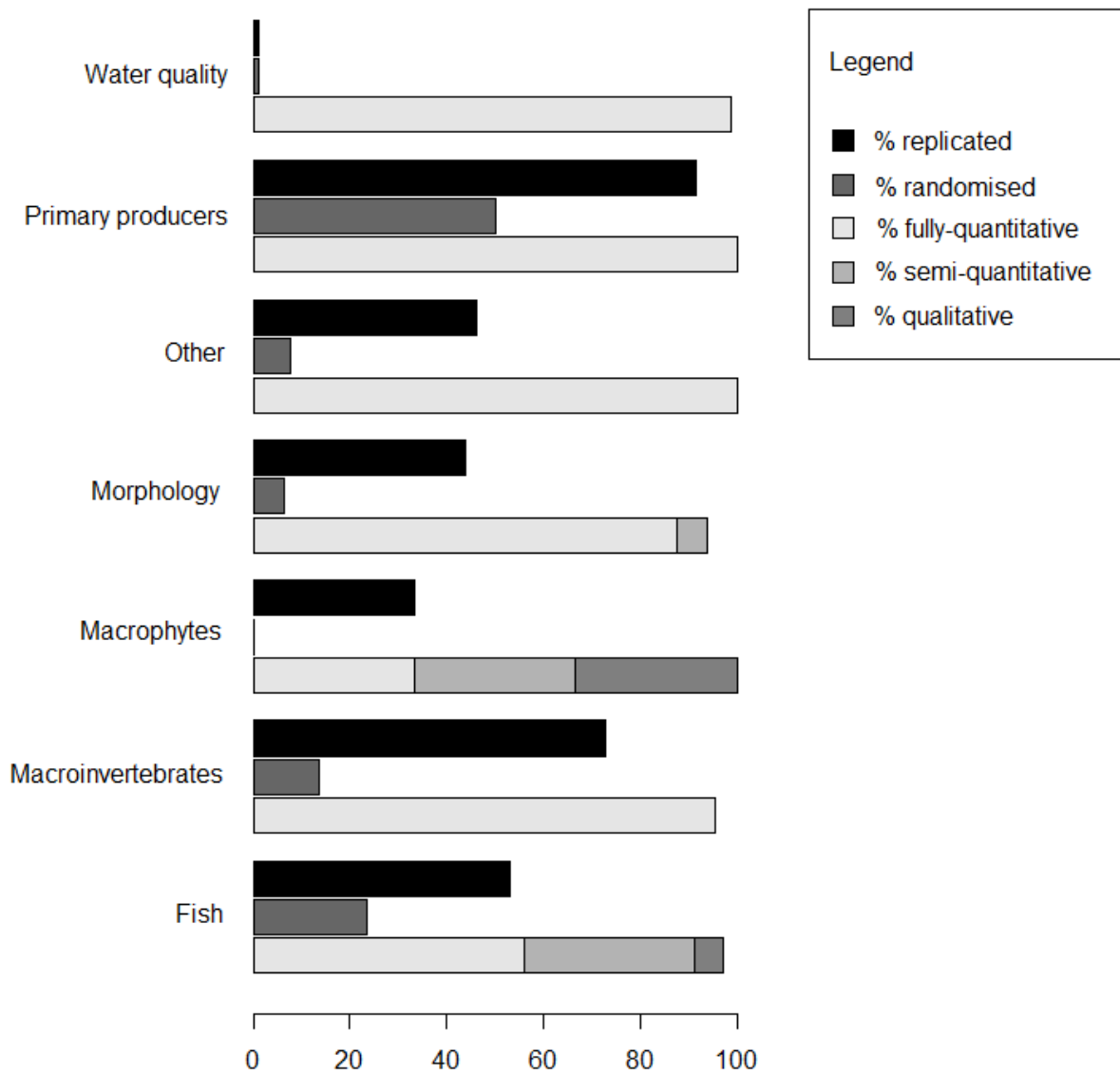


Figure 5 Bar plot of quality assessment indices for each ecosystem response. Note: percentages were calculated based on the total number of reported ecosystem responses; therefore, the sum of quantitative and qualitative percentages is less than 100 where quality assessment indices could not be extracted from a study

823  
824  
825

## Tables

*Table 1: Search terms used in literature search and respective number of results returned.*

Search term	No. results
"reservoir operation"	825
effects AND hydropower	749
"selective withdrawal"	202
"reservoir release*"	200
"varying flows"	182
"pulse release*"	154
"controlled flood*"	129
"artificial flood*"	124
"dam operation"	124
"environmental flow*" AND dam	112
"experimental drought*"	110
"artificial flow*" NOT flower*	97
"flushing flow*"	93
"experimental flood*"	89
"hydropeaking"	83
"environmental flow*" AND reservoir	67
"dam release*"	65
"managed flood*"	56
"e-flows"	50
"artificial release*"	42
"flow alteration*" AND dam	42
"artificial drought"	40
"hydrop* flow*"	34
"planned flood*"	22
"altered flow* regime"	21
"flow alteration*" AND reservoir	21
"reservoir flushing"	20
"peaking flow*"	20
"scour* flow*"	18
"flood program"	18
"hydro-peaking"	17
"test flood*"	16
"hydropower peaking"	15
"environmental flow*" AND impoundment	14
"altered flow*" AND reservoir	11
"spate flow*" NOT flower*	10
"environmental release*" AND reservoir	10
"fluctuating flow*" AND dam	10
"peaking discharge*"	10
"flow alteration*" AND impoundment	9
"scour* flood"	8
"regulated flood"	8
"modified flow* regime"	7
"experimental low flow*"	7
"fluctuating flow*" AND reservoir	6
"dam reoperation"	3
"fluctuating flow*" AND impoundment	3
"spate flood*"	2
"dam re-operation*"	2
"environmental release*" AND dam	2
"reservoir reoperation"	1
"artificial low flow*"	1
"spate release*"	0
"scour* release*"	0
"reservoir re-operation"	0
"impoundment reoperation"	0
"impoundment re-operation"	0
"modified flow* AND reservoir"	0
"environmental release*" AND impoundment	0

Table 2: Total number of studies that reported on each flow modification type, number of studies that reported decreases, no changes or increases in biotic and abiotic ecological responses and most common ecological responses reported from a literature review of 76 studies. Where possible, reports are split between impacts of single (S) and cumulative (C) flow modifications. Study ID's are shown in parentheses (see Appendix 1 for study details).

Flow modification type most emphasised by study (Poff & Zimmerman)	Biotic responses					Abiotic responses			
	Total no. studies	No. studies reporting reduced ecological responses	No. studies reporting no changes	No. studies reporting increased ecological responses	Common ecological responses	No. studies reporting change	No. studies reporting no change	Common ecological responses	
Magnitude	S	55	12	14	21	No change in fish movement (10,18,31,35,37,60,75) Increased fish movement (15,18,27,35,37,57) No change in fish abundance (13,65,72,75) Increased macroinvertebrate drift (17,20,42,43,48,62) Reduced macroinvertebrate density (34,48,61,63,54)	32	9	Increased turbidity (6,7,34,49) Increased suspended solids concentration (14,25,32,34,56,63,68,73) Reduced electrical conductivity (19,34,56,73) Increased bedload transport (12,24,36,55,59,66,68) No change in temperature (34,37,45,63) Increased temperature (18,22,37,42,51)
	C	21	14	9	10	Reduced macroinvertebrate density (20,29,43,45,63,64) Reduced periphyton mass (21,26,30,45,74)	4	0	n/a
Rate of change	S	2	1	1	1	n/a	0	0	n/a
Duration	S	2	1	0	1	n/a	1	0	
Draw-off depth	S	1	0	0	0	n/a	1	0	n/a
Range	C	2	1	1	2	n/a	0	0	n/a



Table 3: Conclusions drawn from this analysis of literature compared with those of Poff & Zimmerman (2010); † - noted in both studies; ¥ - alternative noted in Poff & Zimmerman (2010); ⚡ - not assessed by Poff & Zimmerman (2010). Recommendations for further research and literature analysis associated with conclusions drawn from this study are also noted where applicable.

Conclusions	Recommendations
<b>Spatial distribution of studies</b>	
Spatial bias identified (⚡)	Prioritise areas where reservoir density is high and published research is currently limited
<b>Flow and ecosystem response types</b>	
Increased flow magnitude modification was main focus of studies (†)	Diversify flow modification types assessed Assess impact of reduced flow magnitude
Generally, good variation in ecosystem response types assessed, but a bias towards traditionally monitored types was identified (e.g. fish; water quality) (⚡)	Diversify ecosystem response types assessed
<b>Qualitative flow-ecosystem response relationships</b>	
Reservoir outflow modification has potential for use as management technique, but site-specific factors appear to be important (⚡)	Focus on development of regional, or ecosystem 'type' based understanding rather than global scale (Poff & Zimmerman, 2010)
Long-term ecosystem response to both single- and cumulative- flow modifications unclear (⚡)	Focus on long-term studies in a variety of locations (Poff & Zimmerman, 2010)
Abiotic responses: lack of monitoring post-flow modification (⚡)	Focus on assessment of both during and post-flow modification
<b>Quantitative flow-ecosystem response relationships</b>	
Biotic ecosystem response: no clear trends identified (¥)	Conduct more studies to allow for site-specific factors to be accounted for in future reviews of quantitative flow-ecosystem response relationships
Abiotic ecosystem response: general linear flow modification: ecosystem response identified for EC and SSC, however, not statistically significant (⚡)	
No threshold flows identified (†)	
Limited number of data points restricted statistical analysis (†)	Conduct more studies to enable both identification of trends and statistical analyses to be undertaken
Detail on potential confounding factors was not typically provided (†)	Provide detail on potential confounding factors to enable robust modelling of flow-ecosystem response relationships
<b>Quality assessment</b>	
Majority of papers used fully-quantitative methods for at least one ecosystem response (⚡)	
< 60% of assessments of fish or macrophytes were fully-quantitative (⚡)	
> 60% of studies stated using replication, however only 25% stated using randomisation; this varied by ecosystem response type (⚡)	Increase use of replication and randomisation, especially for assessment of water quality response
Analyses were typically simple one-way ANOVA which failed to take into account temporal autocorrelation (⚡)	Use contemporary models to take autocorrelation into account where necessary
Few studies used control sites (⚡)	Use control sites and BACI designs where appropriate
Both unregulated and regulated river types used as control sites (⚡)	Assess the optimal control site 'type'
Few studies noted statistical power (⚡)	Future research report statistical power
Inconsistent use of terminology within the literature (⚡)	Use "reservoir" and "environmental flow" keyword terms where possible